THE MIDDLE PALAEOZOIC SQUAMULATE FAVOSITIDS OF VICTORIA

by G. M. PHILIP

ABSTRACT. Of the thirteen nominal species of squamulate favositid described from the Middle Palaeozoic of Eastern Australia and New Zealand, two, *Favosites squamuliferus* Etheridge 1899 and *F. grandiporus* Etheridge 1890, are recognized as discrete species, and one closely related non-squamulate species, *F. moonbiensis* Etheridge 1899, is also recognized. *F. squamuliferus* is interpreted as an extremely variable species containing eight arbitrarily separated formae. Eleven European and Russian species are noted which fall within the range of variation of *F. squamuliferus* and *F. grandiporus*. Favositid wall structure and septal apparatus are also discussed.

INTRODUCTION

THIS study arose during the description of a coral fauna from the basal Devonian (?) Limestones outcropping along the Tyers River, Gippsland, Victoria. As work progressed the squamulate favositids of this fauna were found increasingly difficult to classify in terms of existing Australian 'species' until it was realized that the only satisfactory treatment was to regard them as constituting a single species exhibiting remarkably gross intraspecific variation. Attention was then turned to the favositids occurring in some of the higher Devonian limestone horizons of Victoria, those of the Lilydale Limestone (of upper (?) Lower Devonian age) and of the lower Middle Devonian of Buchan and Bindi. Although the favositids of these horizons have not been investigated in the same detail as those of the Tyers River limestone, the same general conclusion is suggested by the material to hand—that the squamulate favositids show such great variation that satisfactory separation into the previously defined 'species' proves impossible in a moderately large collection.

Intraspecific variation in corals. Very little has been done on the variation of tabulate corals. Jones (1936), in studying the three Silurian species *Favosites gothlandicus* Lamarck, *F. forbesi* E. & H., and *F. multiporus* Lonsdale, considered them to be conspecific and recognized them merely as 'formae' within the species *F. gothlandicus*. Jones considered the variation between the forms to be due solely to environment.

More work has been done on variation in rugose corals. Wells (1937) described in detail variation within the Middle Devonian rugose coral *Heliophyllum halli* E. & H. and in place of eight previously described species recognized the single species with one variety and eleven 'formae' between which there was found to be continuous variation. Wells analysed the possible causes of variation and summarized earlier work on variation in corals. Olliver (1958) described the variation in external form of another Devonian rugose coral *Metriophyllum exiguum* (Billings) and recognized six formae 'which form an intergradational system'.

Certainly more examples of variation have been described in scleractinians, particularly Recent forms. The work of Vaughan (1907) on *Porites compressa*, a living hermatypic coral from Hawaii, should be mentioned. Besides the typical form, Vaughan recognized sixteen formae and four sub-formae between which there is continuous

[Palaeontology, Vol. 3, Part 2, 1960, pp. 186–207, pls. 30–34.]

variation. Further, the difficulty encountered in the definition of species of certain living hermatypic scleractinians is well known. Thus Bernhard (1901) experienced so much difficulty in cataloguing Recent corals in the British Museum (Natural History) that he abandoned the binomial system of nomenclature and substituted a geographical number system.

Nominal species and varieties of squamulate favositids. The following thirteen nominal species and varieties have been proposed for squamulate favositids from various localities from the Lower and Middle Devonian of Eastern Australia and New Zealand:

Favosites grandipora Etheridge 1890.
Favosites squamulifera Etheridge 1899.
Cannapora australis Chapman 1908.
Favosites nitida Chapman 1914.
Chaetetes stelliformis Chapman 1918.
Favosites (*Emmonsia*) *spinigera* Chapman 1921 (*non* Hall 1879).
Alveolites victoriae Chapman 1921.
Alveolites regularis Chapman 1921.
Favosites murrumbidgeensis Jones 1937.
Favosites bryani Jones 1937.
Favosites nitidus var. *medius* Hill and Jones 1940.
Favosites ovatiporus Hill and Jones 1940.
Favosites pluteus Hill 1950.

To these may also be added *Favosites basaltica* var. *salaebrosa* Etheridge 1899, although Hill (1950) considered that this form does not possess squamulae. However, prior to now, squamulae have not been recognized as such in six of the species listed above.

Of the species which have been proposed, *F. grandiporus* and *F. squamuliferus* are retained while the rest are regarded as synonyms of one or the other, although some of the names have been retained in the description of formae within *F. squamuliferus*. *F. moonbiensis* Etheridge 1899, the non-squamulate counterpart of *F. squamuliferus*, is also regarded as a discrete species, mainly, however, for simplicity of nomenclature.

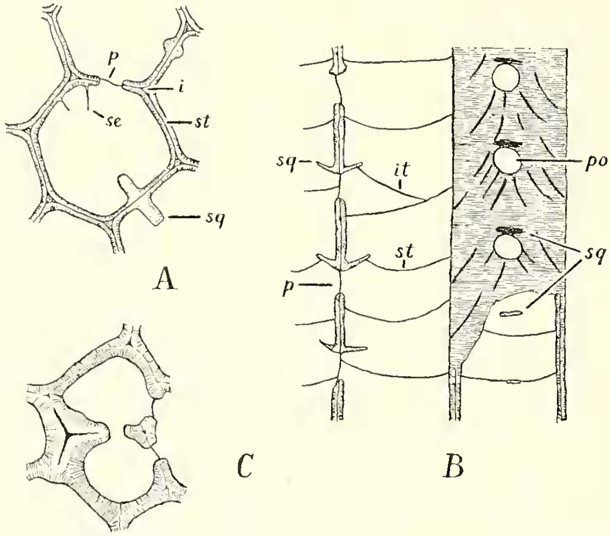
MORPHOLOGY

The main factor common to the above species is that they possess comparatively large mural pores usually in a single row toward the centre of each corallite face. Occasionally they may become widely biserial when the corallite face is wide. In most members of the group squamulae are developed above the mural pores, apparently bearing some relation to them. Thus in these characters most members of the group bear resemblance to *Alveolites battersbyi* E. & H., the type species of the genus *Caliapora* Schlüter 1889. Descriptions of the wall structure and septal apparatus of the members of the group are given in some detail as they have considerable bearing on the question of the generic placement of the group as well as on favositid taxonomy generally.

A. *Wall structure*. Swann (1941; 1947) in his description of the *Favosites alpenensis* lineage recognized the presence of calcareous deposits between the corallite walls of certain favositids. The deposits are distinct from the very thin primary walls and peripheral stereozones of the corallites. They are usually differently stained from the calcite of the peripheral stereozones and so are fairly obvious when they occur. Swann (1947) designated these median wall deposits as the 'intramural coenozone' considering that as such they represented the presence of a coenosarc in favositids.

Deposits between the walls of adjacent corallites in favositids had been noted prior to this. Nicholson (1881, p. 21) in his description of *Favosites inosculans* stated: 'The line of demarcation between the sclerenchyma of any tube and that of its neighbours is in general recognizable by the presence of a clear linear space. . . .' This is well shown in his figures of this species. Etheridge (1899*a*, p. 21) also noted the occurrence of intermural deposits towards the corners of the corallites in *F. moonbiensis* and described them as a 'light clear spot in the wall substance'. Lecompte (1936) also noted such deposits and applied the term 'fissure axiale' to them.

Hill (1950) convincingly rejected Swann's idea that intermural deposits were organic structures, for, as Hill comments, the 'coenozone', as described by Swann, does not possess the fibrous structure which is characteristic of all coral material other than the epitheca. Hill suggested that this coenozone was a phenomenon of fossilization caused



TEXT-FIG. 1. Generalized morphology of *F. squamuliferus* and *F. grandiporus* $\times 20$ approx. A, *F. squamuliferus* forma *bryani* based on T.S. 891. Transverse section; Tyers River limestone. B, *F. grandiporus* showing well-developed 'stellate' intermural space with thickening and bleaching of the stereome of the neighbouring corallites in its vicinity. (From T.S. 1209.) Transverse section; Lilydale Limestone. C, *F. squamuliferus* forma *bryani* based on T.S. 917. Longitudinal section; Tyers River limestone. *i*, intermural space; *p*, mural pore with pore plate; *po*, mural pore; *se*, septal spine; *sq*, squamula; *it*, incomplete tabula; *st*, suspended tabula.

by recrystallization along the junction of two scts of fibres. She noted that a similar structure is present along the median line of the septa in specimens of the rugose coral *Pycnactis* from the Silurian of Great Britain.

Ross (1953) substituted the term 'intermural spaces' for Swann's 'intramural coenozone', also considering that Swann's reasons for regarding them organic in origin were unsatisfactory. Ross concluded that, as the spaces were developed between adjacent corallites in particular growth zones, they were produced as a response to adverse environmental conditions.

The author is in agreement with Ross as to the cause of intermural spaces for the same reason (Pl. 34, fig. 3). Furthermore, within the Victorian squamulate favositids they are so consistently developed that it is hard to imagine them as merely due to fossilization, particularly as other species of *Favosites* occurring side by side with *F. squamuliferus* may not show any development of intermural deposits. In *F. squamuliferus* forma *australis*, a form characterized by subcerioid growth of the corallum, all degrees of development of intermural spaces can be found. In places the corallites are widely separated and elsewhere the walls of adjacent corallites are directly in contact so intermural spaces cannot occur (Pl. 33, fig. 5). Again, with the peculiar 'stellate' intermural spaces discussed below, the stereome of corallites in their immediate vicinity is often bleached and thickened (Pl. 33, figs. 6, 9; Pl. 34, figs. 4, 5; text-fig. 1c). This would be unlikely were intermural deposits merely a fossilization phenomenon.

The intermural spaces of *F. grandiporus* and *F. squamuliferus* and of the closely related non-squamulate *F. moonbiensis* are of a peculiar type. These spaces have already been described by Etheridge (1899*a*) in the latter species. In this type of intermural space the zone of usually almost clear calcite at the junction of walls of adjacent corallites may appear as a very thin band sometimes enclosing whole corallites (Pl. 33, fig. 12), but more often is more or less confined to the junctions of three or more corallites (Pl. 33, figs. 2, 6–11; text-fig. 1A) although the spaces may irregularly expand elsewhere. When the spaces are confined to the angles of the corallites, they may give rise to 'stellate' structures within the walls (Pl. 33, figs. 6, 9) which may be accentuated by bleaching and thickening of the stereome in their immediate vicinity (Pl. 33, figs. 6, 9; text-fig. 1c). In poorly preserved specimens which have suffered marked recrystallization the 'stellate' structures are often strongly emphasized.

This type of 'stellate' wall structure has been described before in various species of *Favosites*. Swann (1947) noted intermural spaces 'thickening greatest at the corners of the corallites' in *F. warthini*, a species showing strong rounding of the corallites. Similar 'stellate' swellings within the walls at the junctions of corallites have been referred to by various authors, although no explanation has been given as to their nature. Examples are:

Favosites asteriscus Frech (Frech 1899, p. 234), a squamulate species, Middle Devonian, China; *F. proasteriscus* Charlesworth 1914, Lower Devonian, Eastern Alps; *F. stellaris* Chernyshev 1937, Devonian (?), Novaya Zemlya; *F. interstinctus* Regnéll 1941, Siluro-Devonian, Tien-shan. Regnéll also gave a comprehensive survey of 'stellate structures' and described them in *Thamnopora tubifera*.

Porfiriev (1937) appears to have noted the work of Frech who considered that the possession of such stellate swellings within favositid walls could be regarded as having generic significance. Porfiriev proposed the genus *Asteriophyllum* based on *A. ænigmaticum*, a species differing only in this respect from *Favosites*.

As 'stellate swellings' appear to be caused by the pulling apart of the walls of adjacent corallites particularly at their corners and the thickening of the stereoplasm of the corallites in their vicinity and were probably developed due to adverse environmental conditions, it is doubtful whether their possession should be regarded as being of generic significance in favositids. Naturally, when cylindrical corallites are packed into a cerioid growth habit, the walls at the corners are not so closely in contact as elsewhere (Pl. 33, fig. 5). Some species exhibit this more than others. For this reason the genus *Asteriophyllum* is best regarded as a synonym of *Favosites*.

Even greater taxonomic importance has been placed on the presence of intermural spaces in favositids. Recently Lafuste (1958, p. 412), on the basis of Swann's (1941) description of favositid wall structure, states of his separation of *Thecia* E. & H. from the Favositidae: 'It is convenient to set apart from *Thecia* the forms which possess a wall of the kind which Swann described in *Favosites*, i.e., a median lamella, two thin dark planes on each side, and two borders of perpendicular fibres. Such a microstructure disagrees with the trabecular constitution of *Thecia* chiefly by its continuity along the periphery of the corallites. . . . It is therefore impossible to agree with Hill and Stumm, who put *Thecia* in the family Favositidae.' Thus even family significance has been placed on a character which at the best can be regarded as being developed as a response to environment.

B. *Septal apparatus*. (i) *Septal spines*. The septal apparatus of *F. squamuliferus* is one of the most variable characters of a particularly variable species. Thin discrete septal spines may occur together with squamulae (Pl. 33, figs. 1, 3; text-fig. 1A). The septal spines are remarkably sporadic in their occurrence and are often present only in certain parts of a corallum. Their presence or absence bears little or no relationship with the various formae of *F. squamuliferus* and they have no correlation with the stratigraphic occurrence of the species. That they have not been observed in certain specimens could well be due to poor preservation, but this cannot be argued for most of the material examined. They are apparently absent in some of the formae of *F. squamuliferus*, but this is most likely due to the small number of specimens so far examined belonging to those formae.

(ii) *Squamulae*. The term 'squamula' as used here implies merely a horizontally flattened, usually blunt septal spine (see text-fig. 1). There can be no doubt that squamulae represent modified septal spines. The view of earlier authors (e.g. Nicholson 1879; Smith and Gullich 1925; Jones 1936; Weissermel 1939) that squamulae were a form of 'degenerate' tabulae appears to have been based partly on a misconception as to their nature. Nicholson, for example, considered what are undoubtedly broken tabulae to be squamulae in *F. forbesi*. Swann gave the following observations in support of the septal nature of squamulae: 1, Squamulae, in common with septal spines, are continuous with peripheral stereozones of corallites. 2, Squamulae are arranged in vertical rows similar to septal spines. 3, Squamulae were apparently secreted by the polyp well up from the basal disc. Swann did not mention the trabeculate nature of squamulae which had been earlier established by Kraicz (1937) in *F. hemisphaericus* var. *bohemicus* Počta. It has also been discussed by Hill (1950) in describing some Australian favositids.

Although squamulae had been recognized by Etheridge (1899*a*) in his description of *F. squamuliferus* they had not been recorded as such in any of the other closely related nominal species till Hill (1950) drew attention to their occurrence in *F. stelliformis* (Chapman), *F. bryani* Jones, and *F. murrumbidgeensis* Jones, as well as in a new species *F. pluteus*. Hill distinguished two types of squamulae—'eaves-like' squamulae which occur in the first four of the above species, and 'shelf-type' squamulae typical of *F. pluteus*. The 'eaves-like' squamulae occur back-to-back in adjacent corallites above each mural pore, as they are developed from the fibrous stereome of the upper margin. They are generally upwardly directed and thicken toward their base. The 'shelf-type' squamulae, on the other hand, consist of horizontal plate-like projections of uniform thickness often bearing no relation to the mural pores and so not developed back to back on opposite sides of the walls.

An examination of a collection of specimens from various localities in Victoria in addition to the large collections from the Tyers River limestone suggests that this distinction cannot be maintained. The shape of squamulae and their relation to the mural pores is extremely variable even in different parts of the one corallum. Even a specimen illustrated as *F. pluteus* by Hill (1949, pl. 8, fig. 26*a*, *b*; M.U.G.D.T.S. 649) shows 'shelf' squamulae occurring side by side with 'eaves' squamulae. In this slide the uniform thickness of many of the squamulae is apparently due to the deposition of an uneven layer of secondary calcite (Pl. 31, fig. 5). Further, in some specimens upwardly directed tapering squamulae may bear no relation to the mural pores (Pl. 31, fig. 1) while in still others thin flat squamulae may occur back to back in adjacent corallites (Pl. 31, figs. 6, 8). There is perhaps a trend for the squamulae to lose their relationship with the mural pores and become longer and thinner, as forms showing squamulae of this type are more common in the Middle Devonian of Buchan and Bindi than at the base of the Devonian. Confirmation of this would lie in a detailed examination of our Middle Devonian favositids. It should be pointed out that Hill (1954) was unable to uphold the separation of *F. pluteus* from *F. bryani* in her description of the coral fauna from Waratah Bay.

One specimen showed a further variation in the squamulae. T.S. 892 (Pl. 31, figs. 1, 2) shows the cross-sections of the cut ends of the squamulae where the section passes close to the plane of the corallite wall. In places this section of the squamulae can be seen to be circular, and so they may be regarded as discrete septal spines. It can be seen also that this is not consistent even within the one section; in other places they are flattened in cross-section.

The degree of development of squamulae can be seen to have been related to the rate of growth of the corallum. In zones where the tabulae are closely spaced (i.e. apparently zones of slow growth) the squamulae are usually strong and moderately closely spaced; in zones of rapid growth with distant tabulae the squamulae may be reduced so as to appear absent in parts of the corallum (Pl. 30, fig. 3). The 'species' *F. ovatiporus* Hill and Jones 1940 is based on a corallum showing well-spaced tabulae and a virtual absence of squamulae, together with large, ovate mural pores (Pl. 32, figs. 1, 2) the shape of which again appears to be a function of the rapid growth of the corallum. This, in fact, can be seen in the one section; portions of T.S. 913 and T.S. 1031 (Pl. 34, fig. 1) show well-spaced tabulae and large ovate mural pores and reduced squamulae while other zones of the coralla have the appearance of *F. nitidus* with closely spaced tabulae, moderately strong squamulae, and comparatively small mural pores. The variable development of squamulae can be pointed to in *F. grandiporus* also. This species has typically a sub-digitate corallum with a rapidly grown axial zone and a more slowly grown distal region. In the axial part of the corallum the squamulae are small and slender, whereas distally they are thick and large (Pl. 32, figs. 6, 7).

The taxonomic importance of the presence of squamulae should also be discussed. Hill (1950) with reservation placed the species *F. moonbiensis* Etheridge in the synonymy of *F. bryani* (here regarded as a forma of *F. squamuliferus*) as she noted the two were indistinguishable except that *F. bryani* possessed squamulae. If the two species are not very closely related then we have here a remarkable case of virtually isochronous parallelism, particularly in view of the fact that both possess intermural deposits confined to the corallite corners (cf. Pl. 31, fig. 3 and Pl. 33, fig. 2 with Pl. 31, figs. 2, 4, 7 and Pl. 33, fig. 3). Extensive collecting from the limestones and underlying mudstones along the Tyers River showed that *F. moonbiensis* is one of the most common favositids of the mudstone facies, whereas it is completely absent in the overlying limestones. On the other hand, the various formae of *F. squamuliferus* are confined to the limestone facies except for two isolated coralla collected in the upper, more calcareous phases of the mudstone. (For further details of the distribution of these species see Philip 1960.) The few other localities in Eastern Australia from which *F. moonbiensis* has been recorded should be investigated to find whether this facies relationship exists elsewhere. This relationship between *F. squamuliferus* and *F. moonbiensis* suggests that squamulae in the Victorian forms were developed as a response to gross environmental changes. This view is perhaps supported by the fact that in longitudinal sections of *F. moonbiensis* swellings in the stereome of the walls above the mural pores are sometimes encountered. These could well represent 'incipient' squamulae (Pl. 31, fig. 3).

This whole discussion raises the question of the relationship of *Favosites* to *Caliapora* Schlüter and *Emmonsia* E. & H. Hill and Stumm (1956, p. F464) define *Caliapora* to include forms 'like *Emmonsia* but with squamulae with concave upper surfaces'. As has been already stated and is obvious in an examination of the plates, the group dealt with here exhibits such extreme variation in the shape of squamulae that even specific significance cannot be placed on this feature. It seems then that *Caliapora* cannot be separated from *Emmonsia*. Schouppé (1951; 1954*a*) has continued to regard *Caliapora* as a subgenus of *Alveolites*. There appears to be certain justification in regarding *Caliapora*-like forms as being related to *Alveolites* for certain species (e.g. *Alveolites fornicatus* Schlüter) usually placed in that genus are very similar morphologically to the type species of *Caliapora*.

None of the more recent authors who have upheld the generic status of *Emmonsia* has doubted the polyphyletic origin of species placed in this group. Smith and Gullick (1925) explicitly stated that the genus is polyphyletic, 'an assembly of polygerontic forms exhibiting a form of degeneration common in many lineages of *Favosites*'. This view is again expressed by Fenton and Fenton (1936), Swann (1947), and Stumm (1949). Great difficulty has been encountered in the application of the genus. Fenton and Fenton (1936, p. 22) would retain '*Favosites* for forms in which $\frac{2}{3}$ of the tabular structures are complete (tabulae) and introduce *Emmonsia* when squamulae number more than $\frac{1}{3}$ the total . . .', a procedure which appears arbitrary in the extreme. Ross (1953) overcame the difficulty of the polyphyletic origin of the genus by employing *Emmonsia* as a genomorph of *Favosites* in the sense in which the concept was introduced (Smith and Lang 1930) for a morphological stage which occurs in different lineages. In dealing with the present group of favositids it is doubtful whether even this procedure is justified, as squamulae here were apparently developed as a response to gross environmental changes.

It should be noted that Swann (1947) suggested as a new generic character of *Emmonsia* the alternation of squamulae with mural pores, but Ross (1953) has shown (as also did Swann) that this character is developed in different lineages of the North American favositids.

The present conclusion, then, is that *Caliapora* Schlüter and *Emmonsia* E. & H. are best regarded as synonyms of *Favosites*, and the application of *Emmonsia* as a genomorph is not justified in dealing with the Eastern Australian Devonian favositids.

F. grandiporus Etheridge possesses a subdigitate corallum and also shows considerable distal thickening of the corallite walls (Pl. 32, figs. 6, 7). In these characters it approaches species which are generally referred to *Thamnopora*. Swann noted a similar case in his description of *F. alpenensis* lineage. One offshoot from the main lineage, *F. dumosus* Winchell, possesses the same distal thickening and growth habit as *Thamnopora*. This again suggests a possible polyphyletic origin of species included in *Thamnopora*.

The Upper Carboniferous North American genus *Acaciapora* Moore and Jeffords 1945 differs from *Thamnopora* only in the possession of squamulae. Out of the context of its relationship with *F. squamuliferus*, *F. grandiporus* could be placed in this genus, if separation of this genus were considered justified.

METHOD OF STUDY

The fauna investigated in detail was taken from the limestone horizon exposed in the valley of the southern part of the Tyers River, Gippsland, Victoria. Precise correlation of this fauna with overseas sections is difficult, but it is best regarded as being of basal Devonian age. Coralla were collected from various localities in the limestone which reaches a maximum thickness of less than 200 feet. In view of the fact that *F. squamuliferus* is a long-ranging species (from Upper Silurian to Middle Devonian) the coralla were treated as being contemporaneous. This is further justified by the fact that there is no faunal differentiation within the limestone horizon apart from that which can be ascribed to facies changes.

In the early stages of the work, when only a few coralla had been examined, many of the squamulate 'species' listed earlier were recognized in the fauna, but as more and more specimens were examined separation into the previously defined 'species' became wellnigh impossible. Differentiation of these 'species' has proved troublesome before, even in small collections (Hill 1954).

It was found that the only adequate way to characterize the extreme variation of the squamulate favositids within the Tyers fauna, short of illustration of virtually each specimen, was to construct scatter diagrams of the various commensurable characters by which favositid species are defined. A few particularly variable coralla were rejected as it was considered that they could not be defined adequately merely by average measurements.

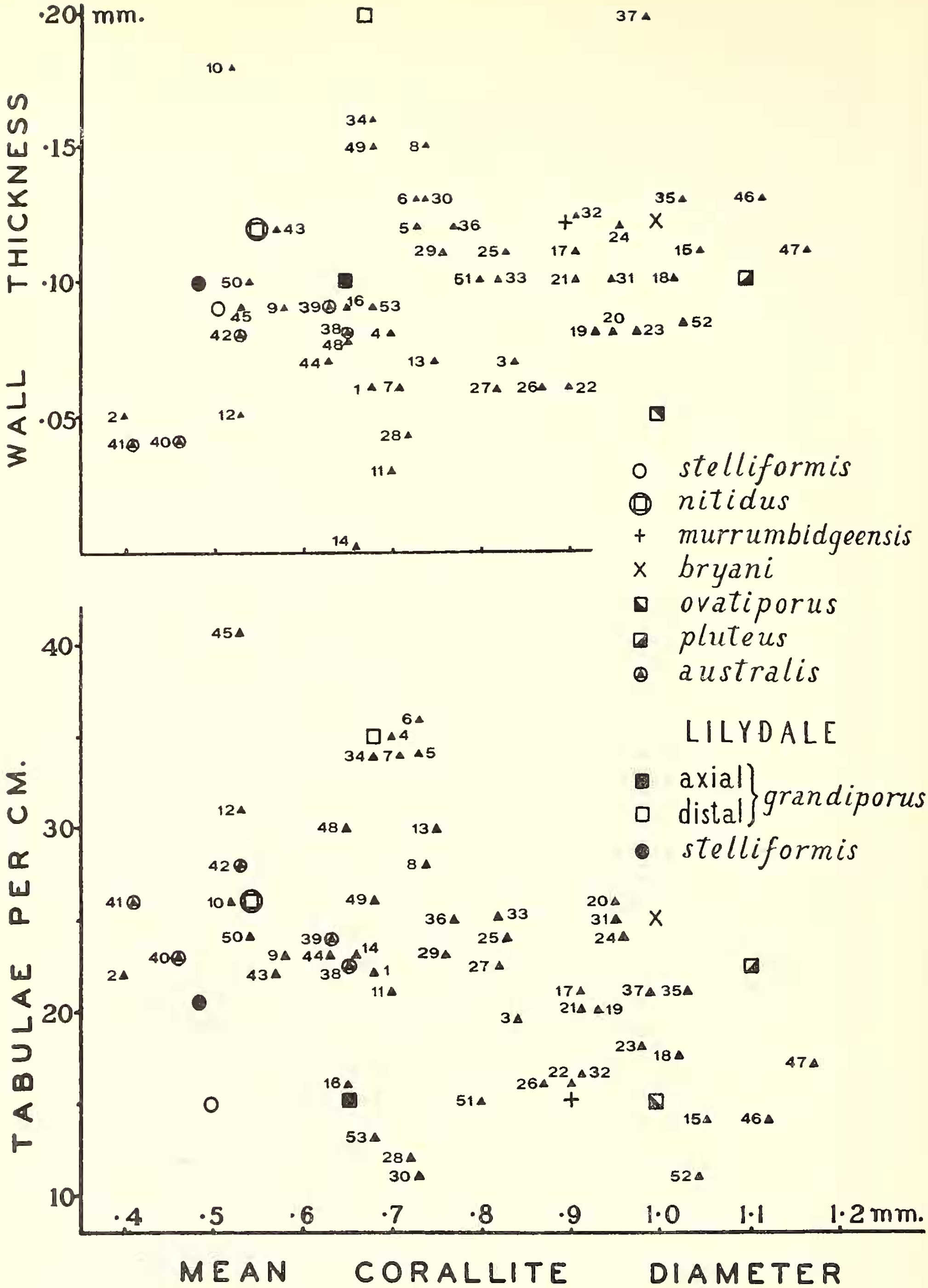
Of the 135 coralla collected, 53 were considered suitable, after the preparation of sections, for the calculation of average measurements. The features determined were:

1. *Mean corallite diameter*. An endeavour was made to measure the maximum diameter of the corallites in thin sections normal to the direction of growth. The diameter was measured from the boundary of the primary walls of the corallites. At times this measurement was made with polished surfaces.

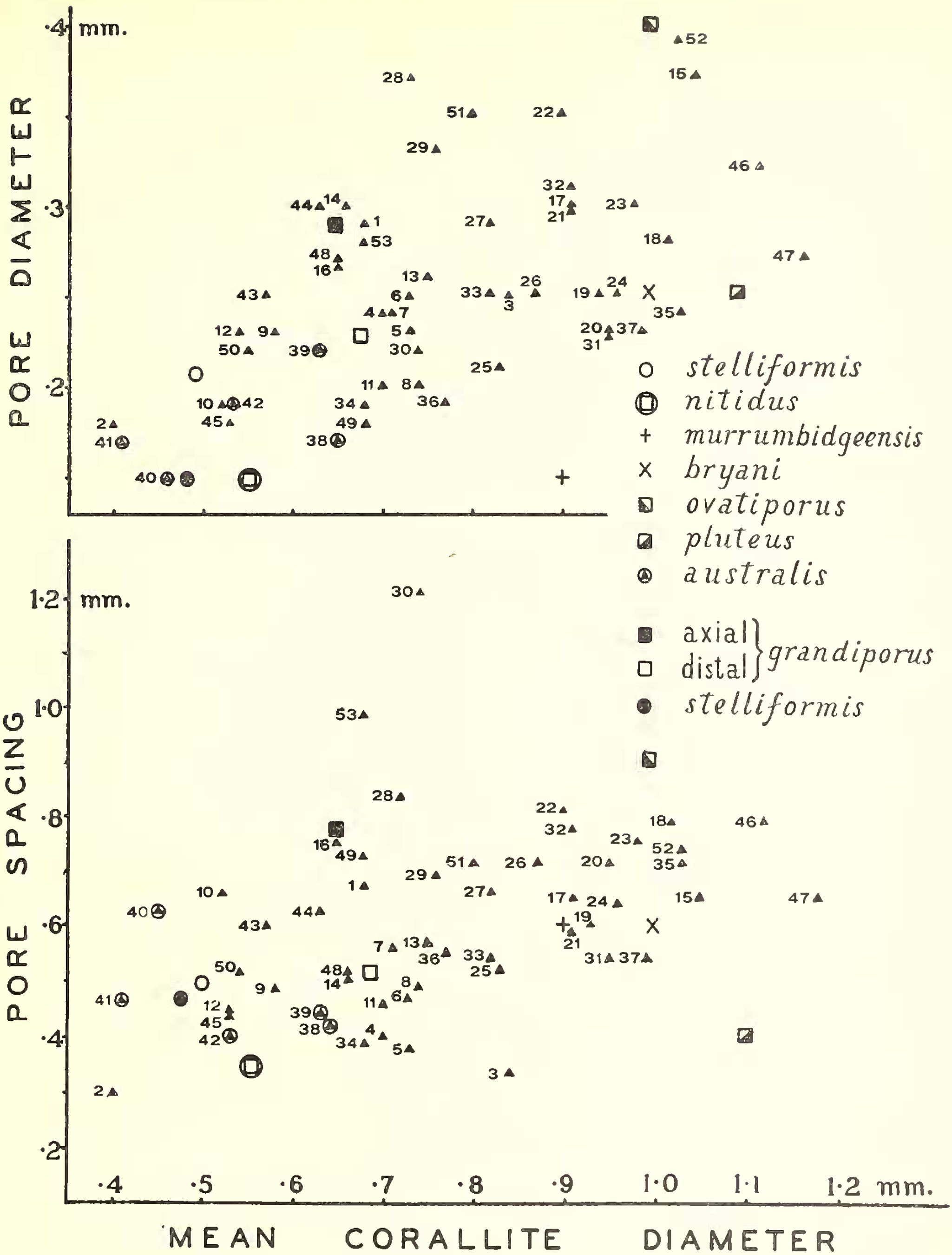
2. *Mean number of tabulae per centimetre*. The number of tabulæ over a comparatively large length of corallites was measured to include the different spacing of tabulae within the one corallum. At least 10 cm. of corallite length was measured for each corallum, and usually the figure was greatly in excess of this.

3. *Mean diameter of mural pores*. The diameter of all mural pores visible in each section was taken. In one case this was as few as six, but usually many more were used. As the mural pores were often oval, the square root of the height by the width was taken as the diameter.

4. *Average spacing of mural pores*. This measurement is the vertical spacing of the centres of mural pores and was arrived at by the addition of half the vertical diameter of two consecutive mural pores and the length of corallite between them. Measurements 3 and 4 were made simultaneously although



TEXT-FIG. 2. Scatter diagrams of the average wall thickness and average number of tabulae per centimetre against the mean corallite diameter for fifty-three specimens of *F. squamuliferus* from the Tyers River limestone. Superimposed are the approximate positions of six of the more commonly used 'species' of squamulate favositid, the positions of which were arrived at from the descriptions and figures of various authors. Specimens of *F. squamuliferus* forma *australis* from the Tyers River limestone are designated by a different symbol. The two illustrated specimens from the Lilydale Limestone are also included. No morphological separation of the fauna into 'species' is possible.



TEXT-FIG. 3. Scatter diagrams of average mural pore diameter and average mural pore spacing against mean corallite diameter for fifty-three specimens of *F. squamuliferus* from the Tyers River limestone. Superimposed are the approximate positions of the more commonly used 'species' of squamulate favositid, which were arrived at from the descriptions and figures of various authors. Specimens of *F. squamuliferus* forma *australis* from the Tyers River limestone are designated by a different symbol. The two illustrated specimens from the Lilydale Limestone are also included. Only an arbitrary separation is possible.

the spacing of the pores was measured also in well-oriented longitudinal sections normal to the corallite faces where the pores are represented by breaks in the walls.

5. *Mean diameter of corallite walls*. This included the total diameter of the walls of two adjacent corallites and in places included intermural spaces. It was measured half-way between the corners of the corallites so as to avoid measurements through the thickened corners in specimens where the corallites were rounded.

An attempt was also made to characterize the orientation and length of the squamulae, but these proved so variable even in the one corallum that this was abandoned.

The thin sections used in the construction of the scatter diagrams are in Melbourne University Geology Department Thin Section Collection T.S. 849 and 861 to 965 inclusive. The average characters arrived at for each of the fifty-three specimens are entered in the thin-section catalogue.

Examination of the four scatter diagrams reproduced here shows that it is impossible to subdivide morphologically this fauna into components between which there is no intergradation. The same is also true of the six other possible scatter diagrams which were constructed. Certain individual specimens may appear to be isolated from the group in one particular character (14, 37—wall thickness; 30—pore spacing; 45—tabulae spacing), but these individuals represent the extreme development of a feature already shown to a lesser degree by other members of the group. The divergent types are represented as formae within the single species.

The scatter diagrams show a certain degree of correlation between morphological features which could be expected on general grounds. For example, with increasing corallite diameter the mural pores generally become larger and more distant while the wall thickness perhaps tends to increase. Another trend which can be seen from the scatter diagrams which are not reproduced here is an increase of the spacing of the mural pores with increase in spacing of the tabulae. Overall, however, it can be seen that there is no great degree of correlation between the various morphological features.

SYSTEMATIC DESCRIPTIONS

Genus FAVOSITES Lamarck

Favosites grandiporus Etheridge

Plate 32, figs. 6, 7; Plate 33, fig. 9; Plate 34, fig. 4; text-fig. 1c

Favosites grandipora Etheridge 1890, p. 61, 2, pl. 8, figs. 6–9.
Alveolites victoriae Chapman 1921, p. 215, pl. 11, figs. 17, 18.

Diagnosis. Corallum subdigitate, cylindrical, sometimes amalgamated by later overgrowths. Corallites gently expanding in axial region, bending sharply to emerge normal to the surface of the corallum; corallites polygonal in axial region, usually rounded distally, diameter averaging between 0·6 and 1 mm.; distally the mural pores are more closely spaced and smaller, the tabulae more crowded, the walls thicker, and the squamulae more strongly developed.

Observations. The measurements of a typical specimen can be seen in text-figs. 2, 3. It may be that this species, differing from *F. squamuliferus* in the growth habit and distal thickening of the corallites, is transitional morphologically with that species. However, the material so far investigated from the Lilydale Limestone, the only horizon from which *F. grandiporus* is known, suggests that it is a separable species. Distal thickening of corallites in tabulate corals is generally regarded as a character of generic merit.

Reference to Chapman's type slides of *Alveolites victoriae* shows that this species is based on a specimen of *F. grandiporus* with comparatively large corallites. In his original description Chapman noted the distal thickening of the walls of the corallites and his plate shows the characteristic wall structure of *F. grandiporus*. Chapman apparently regarded as 'teeth' the remnants of the walls of corallites on each side of a mural pore, as encountered in transverse sections, and so placed the species in the genus *Alveolites*.

Of the well-developed squamulae in this species Jones (1937, p. 93) has stated: 'The appearance of spines in longitudinal section is caused by the breaking down of the wall where the large mural pores almost meet.'

Favosites squamuliferus Etheridge

Favosites squamulifera Etheridge 1899*a*, pp. 166–7, pl. 38, figs. 4, 5.
Emmonsia squamulifera (Etheridge fil.); Jones 1937, p. 99.

Diagnosis (after Etheridge). Corallum massive, corallites approximately the same size, averaging 1 mm. or less in diameter, mural pores small, in a single column on each corallite face; squamulae horizontal or inclined, tabulae moderately closely spaced.

Observations. Etheridge's meagre description and inadequate figures make the interpretation of this species difficult. The type specimens are reported by Hill (1950) to be missing, and there is even some doubt as to the type locality of the species. Not until the tabulate corals of the Tamworth district of New South Wales are investigated in detail will this species be properly understood. Because of this the use of the species here is undesirable, but as it cannot be questioned that it is the first name employed in the literature to this species it is retained.

It is more than likely that *F. squamuliferus* will prove to be identical with *F. bryani* Jones. As *F. bryani* is much more precisely defined, it is retained in the naming of the forma which most probably includes *F. squamuliferus* s.s.

Favosites squamuliferus forma *bryani* Jones (forma α[1])

Plate 31, figs. 1, 2, 4–6, 8; Plate 33, fig. 3; text-fig. 1A, B

?*Favosites squamulifera* Etheridge 1899*a*, pp. 166–7, pl. 38, figs. 4, 5.
?*Favosites gothlandica* Lamarck; Chapman 1920, p. 186 (*partim*), pl. 23, figs. 18, 19.
Favosites (*Emmonsia*) *spinigera* Chapman 1921, pp. 214–15, pl. 9, fig. 21 (*non* Hall 1879, p. 108, pl. 4, figs. 1–5).
Favosites murrumbidgeensis Jones M. S., *in* Allan 1935, p. 7, pl. 4, figs. 5, 6.

[1] The formae recognized within *F. squamuliferus* are designated with a Greek letter, a procedure used by Olliver (1958). Although the 'forma', as used by various authors, has no standing as a taxonomic category and so the laws of priority do not apply, later authors are liable to elevate the names employed as formae to the rank of subspecies. Thus Bassler (1950, p. 81) lists Lecompte's (1939) two formae of *F. goldfussi*, *F. goldfussi* forma *regularis*, and *F. goldfussi* forma *pyriformis* as subspecies, thus presumably making the former a further homonym of *Favosites regularis* (Chapman 1920) along with *F. kennihoenis* var. *regularis* Ozaki 1934, *F. regularis* Jones 1937, and *F. hisingeri* var. *regularis* Ruhkin 1938 and the latter a homonym of *F. pyriformis* (Hall 1852). To avoid such possible contingencies it is best to refrain from applying to new formae names which could be used as trivial appellations.

Favosites bryani Jones 1937, pp. 96–97, pl. 15, figs. 3–6.
Favosites murrumbidgeensis Jones 1937, p. 98, pl. 16, figs. 5, 6.
?*Emmonsia squamulifera* (Eth. fil.); Jones 1937, p. 99.
Favosites bryani Jones; Hill and Jones 1940, pp. 190–1, pl. 5, figs. 2*a*, *b*; Jones 1941, p. 42, pl. 1, fig. 1; Hill 1942, p. 8, pl. 2, fig. 6; Jones 1944, p. 34, pl. 1, figs. 1, 2; Hill 1950, p. 150, pl. 7, figs. 23, 24.
Favosites pluteus Hill 1950, p. 151, pl. 8, figs. 25–26.
Favosites affin. *bryani* Jones; Hill 1954, pp. 113–14, pl. 9, figs. 23, 24.

Material. Specimens 3, 17–21, 23–27, 31–33, 35, 46, 47; figured slides T.S. 891 (18); T.S. 892 (20); T.S. 895 (21); T.S. 917 (31); T.S. 921 (32) and T.S. 649 from Rocky Camp, Murrindal Limestone, Buchan.

Diagnosis. Corallum massive, corallites polyhedral averaging greater than 0·8 mm. diameter and usually less than 1·5 mm.; mural pores uniserial circular to slightly ovate between 0·15 and 0·35 mm. in diameter and between 0·3 and 0·8 mm. apart. Squamulae

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EXPLANATION OF PLATE 30

Longitudinal sections; all figures × 10 and unretouched. The serial number in parentheses refers to the number of the specimen in the scatter diagrams, and the prefix 'T.S.' refers to catalogue numbers in the Melbourne University Geology Department Thin Section Collection of Fossils.

Figs. 1, 2. *Favosites squamuliferus* forma *stelliformis* (γ). 1, T.S. 849 (2). Small corallite diameter, poorly developed squamulae, and well-spaced tabulae developed in places at similar heights in adjacent corallites. Tyers River limestone. 2, T.S. 1211 (also Pl. 33, fig. 6). Well-developed flattened squamulae occurring back to back in neighbouring corallites above mural pores. 'Pore plates', usually present in *F. squamuliferus*, also seen. Lilydale Limestone.

Figs. 3–5, 7. *F. squamuliferus* forma *nitidus* (β). 3, T.S. 875 (9) (also Pl. 33, fig. 7). Variable development of squamulae. 4, T.S. 924 (34) (also Pl. 33, fig. 8). Very closely spaced suspended and 'incomplete' tabulae and thick-based squamulae. 5, T.S. 880 (12). Moderately large mural pores and small squamulae. 7, T.S. 865 (4). Mural pores and small squamulae. All from Tyers River limestone.

Fig. 6. *F. squamuliferus* forma *australis* (δ). T.S. 935 (39) (also Pl. 33, fig. 5). Wide, irregular intermural spaces, well-spaced tabulae, and small squamulae. Tyers River limestone.

Fig. 8. *F. squamuliferus* forma η. T.S. 882 (14) (also Pl. 33, fig. 4). Extremely thin-walled form with small squamulae and well-spaced tabulae. Mural pores also seen. Tyers River limestone.

EXPLANATION OF PLATE 31

Longitudinal sections; all figures × 10 and unretouched.

Figs. 1, 2, 4–6, 8. *F. squamuliferus* forma *bryani* (α). 1, 2, T.S. 892 (20). Strong, upwardly curved squamulae, in places not occurring back to back in adjacent corallites. The cut ends of the squamulae are in places circular rather than flattened. Tyers River limestone. 4, T.S. 917 (31). Short, upwardly directed squamulae, well-spaced tabulae, and a single column of moderately large mural pores. Tyers River limestone. 5, T.S. 649. Slide illustrated as '*F. pluteus*' (Hill 1950, pl. 18, fig. 26*a*, *b*). Note upwardly directed, tapering squamulae above the mural pores. An irregular deposit of secondary calcite can be seen obscuring the taper of the squamulae and giving also the appearance of very thick tabulae. Murrindal Limestone, Rocky Camp, Buchan. 6, T.S. 921 (32). Similar specimen with horizontally directed squamulae, some of which do not occur back to back in neighbouring corallites. Tyers River limestone. 8, T.S. 895 (21). Large, closely spaced mural pores, and thin, delicate squamulae, thus approaching forma *ovatiporus*. Tyers River limestone.

Fig. 3. *F. moonbiensis* Etheridge. T.S. 800 (also Pl. 33, fig. 2), cf. figs. 4, 7. Note similarity between this form and *F. squamuliferus* forma *bryani*. Occasional swellings in the stereome of the walls above mural pores may be encountered (e.g. top right-hand corner of figure). These swellings could represent 'incipient' squamulae. Mudstone beneath the limestone, Tyers River.

Fig. 7. *F. squamuliferus* forma ζ. T.S. 915 (30). Note the small, distantly spaced mural pores, well-separated tabulae, and reduced squamulae. Tyers River limestone.

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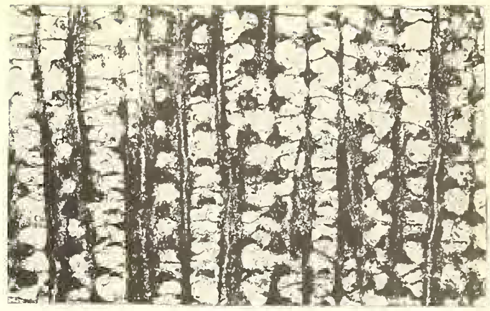

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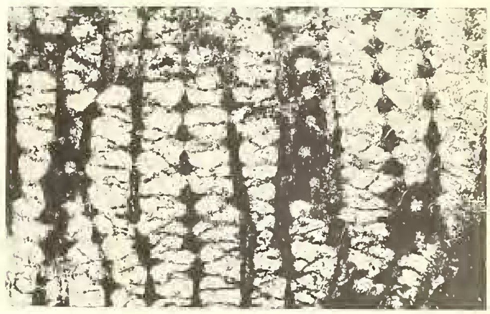

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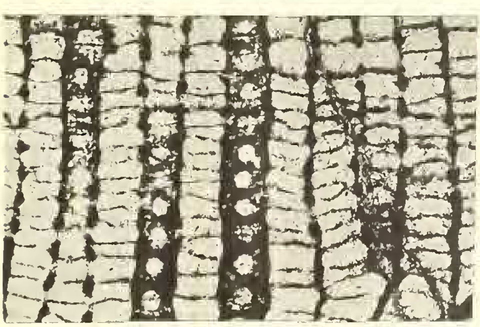

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PHILIP, Australian favositids

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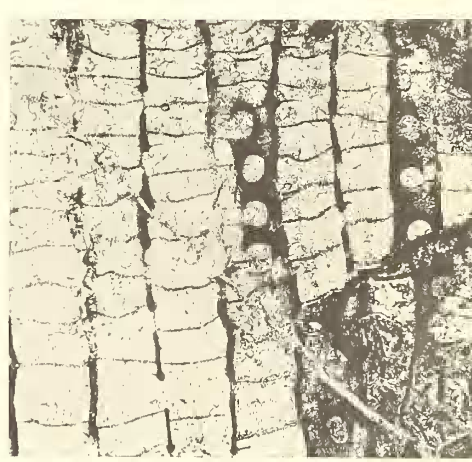

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PHILIP, Australian favositids

highly variable, horizontal or upwardly directed, developed either back to back in adjacent corallites above the mural pores or isolated. Slender septal spines may also be present.

Observations. F. squamuliferus forma *bryani* is arbitrarily separated from forma *nitidus* (β) and forma *stelliformis* (γ) by the corallite diameter. In the forms with smaller corallite diameter the tabulae may be more closely spaced. As can be seen from the synonymy of this species five different specific names have been applied to this forma.

F. squamuliferus forma *nitidus* (β)

Plate 30, figs. 3–5, 7; Plate 34, figs. 1, 7, 8, 10

?*Favosites* sp. indet. Etheridge 1899*b*, p. 33, pl. B, figs. 7–9.
Favosites nitida Chapman 1914, p. 309, pl. 54, figs. 21–23; pl. 55, figs. 24, 25.
Favosites forbesi (*partim*) Chapman 1914, pl. 53, fig. 19 (*non*. pl. 56, fig. 27).
Favosites nitida Chapman; Jones 1937, p. 93, pl. 12, figs. 4, 5.
Favosites nitidus Chapman; Hill and Jones 1940, p. 198, pl. 6, figs. 3*a–c*.
Favosites nitidus var. *medius* Hill and Jones 1940, pp. 198–9, pl. 6, figs. 4*a*, *b*; pl. 7, figs. 1*a*, *b*, 2.
Favosites nitidus Chapman; Jones 1941, p. 43, pl. 1, fig. 2; Hill 1950, pp. 148–9, pl. 7, figs. 20*a*, *b*; Hill 1954, p. 113, pl. 9, figs. 25*a*, *b*.

Material. Specimens 1, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 16, 29, 34, 44, 45, 48, 50, 53; figured slides T.S. 865(4); T.S. 870(6); T.S. 875–6(9); T.S. 880(12); T.S. 924–5(34); T.S. 967; T.S. 1031.

Diagnosis. F. squamuliferus with average corallite diameter between 0·5 and 0·8 mm.

Observations. In general, besides the smaller corallite diameter, this forma has smaller mural pores and may also have closer tabulae than is usual in forma *bryani*.

Hill and Jones (1940) note that there is a complete gradation between *F. nitidus* and *F. salaebrosus* Etheridge 1899 and that *F. salaebrosus* should be set aside for forms having a considerable number of reclined corallites which as a result appear alveolitoid in transverse sections. They proposed *F. nitidus* var. *medius* to include forms intermediate between *F. nitidus* and *F. salaebrosus*. If squamulae prove to be present in the type slides of *F. salaebrosus* then this species could be set aside as a further forma of *F. squamuliferus* to include forms with reclined corallites.

F. squamuliferus forma *stelliformis* Chapman (γ)

Plate 30, figs. 1, 3; Plate 33, fig. 6

Chaetetes stelliformis Chapman 1918, p. 393, pl. 42, figs. 1–3.
Alveolites regularis Chapman 1920, p. 216, pl. 11, figs. 19, 20.
Favosites stelliformis (Chapman); Hill, 1950, p. 149, pl. 7, figs. 21, 22.

Material. Specimen 2; figured slides T.S. 849 (2) also T.S. 1210-1 from the Lilydale Limestone.

Diagnosis. F. squamuliferus with the average diameter of corallites less than 0·5 mm.

Observations. Hill (1950, p. 149), although recognizing the relationship to *F. squamuliferus* forma *nitidus*, suggested by this form from Buchan, states: 'Its unusual characters, the numerous oval pores separated by squamular aggregations of trabeculae and the regular tabular floors throughout the corallum, suggest it might be wise to erect a new genus for it.' The similar height of tabulae in adjacent corallites is fairly common in *F. squamuliferus*, particularly in those specimens with small corallites. The holotype of *F. nitidus* var. *medius* (Hill and Jones 1940, pl. 6, fig. 4*a*) shows this character although perhaps not as strikingly as in the specimens illustrated as *F. stelliformis* by Hill. It should be noted that Chapman's original figures of *F. stelliformis* do not show this at all well, nor do other specimens of this forma from Buchan and Bindi.

F. squamuliferus forma *australis* (Chapman) (δ)

Plate 30, fig. 6; Plate 33, fig. 5; Plate 34, fig. 3

Cannapora australis Chapman 1907, p. 76, pl. 3, figs. 6, 7; pl. 8, figs. 17, 18.

Material. Specimens 38–42; figured slides T.S. 934–5 (39); T.S. 985.

Diagnosis. *F. squamuliferus* with small corallite diameter and sub-cerioid growth allowing separation of the corallites.

Observations. Chapman's type specimens of this species were collected from the Tyers River limestone, but have apparently been lost. The topotype illustrated matches Chapman's figures very closely. Although the corallites may not all be in contact in other formae of this species (a feature which is often difficult to detect even in thin section) extreme cases of this feature appear to be confined to specimens of *F. squamuliferus* with small corallite diameter, well-spaced tabulae, and reduced squamulae.

F. squamuliferus forma *ovatiporus* Hill and Jones (ϵ)

Plate 32, figs. 1, 2

Favosites ovatiporus Hill and Jones 1940, pp. 199, 200, pl. 7, figs. 3, 4; pl. 8, figs. 1, 2; Hill *in* Thomas 1947, p. 41.

Favosites? *ovatiporus* Hill and Jones 1940 var.; Hill 1954, p. 113, pl. 8, figs. 21, 22.

Material. Specimens 15, 22, 28, 51, 52; figured slides T.S. 912 (28) and T.S. 961(51).

Diagnosis. *F. squamuliferus* with large, ovate mural pores greater than 0·35 mm. in diameter, and well-spaced tabulae, usually less than 15 per cm.

Observations. As has been mentioned earlier the squamulae are so reduced in this forma that in places in a corallum they are virtually absent.

EXPLANATION OF PLATE 32

Longitudinal sections; all figures ×10 and unretouched.

Figs. 1, 2. *F. squamuliferus* forma *ovatiporus* (ϵ). 1, T.S. 912 (28). Occasional large ovate mural pores, typically concave distant tabulae, and exceedingly small squamulae. 2, T.S. 961 (51). Stronger squamulae, closer tabulae, and smaller mural pores; i.e. intermediate between forma *bryani* and forma *ovatiporus*. Tyers River limestone.

Figs. 3–5. *F. squamuliferus* forma θ. 3, T.S. 944 (43) (also Pl. 33, fig. 11). Irregularly spaced mural pores, small squamulae, and expanding corallites which give rise to a subdigitate corallum which characterizes this forma. Note also comparatively thicker walls. 4, T.S. 930 (36). Intermediate between forma *nitidus* and forma θ. 5, T.S. 932 (37), (also Pl. 33, fig. 12). Larger corallite diameter again with small squamulae, thick walls, and irregularly distributed mural pores. Clear zones in the middle of the walls represent intermural spaces. Tyers River limestone.

Figs. 6, 7. *F. grandiporus* Etheridge. 6, T.S. 1208 (also Pl. 33, fig. 9, Pl. 34, fig. 4). Axial portion of a large cylindrical corallum. Note comparatively thin walls, well-spaced tabulae and mural pores, as well as small squamulae. 7, T.S. 1205. Distal portion of same corallum, showing strong thickening of the walls, heavier squamulae, and crowded tabulae. Mural pores are also smaller and more closely spaced. Lilydale Limestone.

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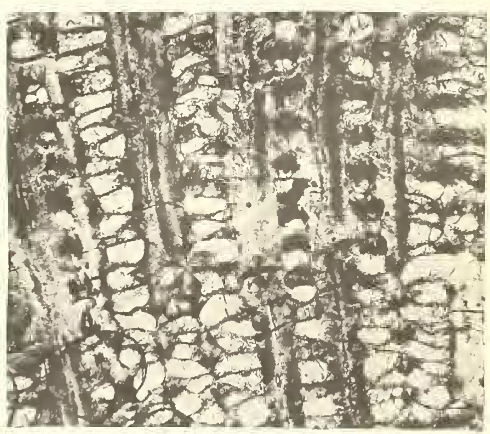

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F. squamuliferus forma ζ nov.

Plate 31, fig. 7

Diagnosis. F. squamuliferus with widely spaced tabulae and reduced squamulae as in *F. squamuliferus* forma *ovatiporus* but the mural pores are comparatively small and average 1·2 mm. apart.

Material. Specimen 30; figured slide T.S. 915 (30).

F. squamuliferus forma η nov.

Plate 30, fig. 8; Plate 33, fig. 4

Material. Specimen 14; figured slides T.S. 882–3 (14).

Diagnosis. F. squamuliferus with very thin walls averaging less than 0·01 mm. thick.

Observations. The single specimen from the Tyers limestone on which this forma is based shows consistently thin walls with a very narrow sporadic stereozone which may thicken slightly at the corners of the corallites. Other specimens (e.g. T.S. 967; Pl. 33, fig. 1) may show in places similar very thin walls, but this was the only specimen collected in which the feature was constant.

F. squamuliferus forma θ nov.

Plate 32, figs. 3–5; Plate 33, figs. 11, 12; Plate 34, fig. 5

Material. Specimens 36, 37, 43, 49; figured slides T.S. 943–4(43); T.S. 930(36); T.S. 931–2 (37); T.S 1013.

Diagnosis. Subdigitate thick-walled *F. squamuliferus* with irregularly spaced mural pores and reduced squamulae.

Observations. This forma perhaps represents a morphological stage between *F. squamuliferus* and *F. grandiporus* since it possesses the subdigitate growth habit and thick walls of the latter species, although it lacks its characteristic distal thickening of the corallite walls.

Apart from the eight formae of *F. squamuliferus* recognized here, *F. salaebrosus* Etheridge should most probably be set aside as a ninth for forms of *F. squamuliferus* with reclined corallites.

It is considered that it is worth separating the species into the various formae since outside of a large collection one forma may appear to be separated from typical members of other formae by differences of specific merit.

COMPARISON OF *F. GRANDIPORUS* AND *F. SQUAMULIFERUS* WITH NON-AUSTRALIAN SPECIES

Certain species have been described from the Upper Silurian to Middle Devonian limestones in Europe and Russia which fall in the morphological range of the species *F. grandiporus* and *F. squamuliferus* as these variable species must be understood. This list is probably by no means complete as the writer has been unable to trace most of the recent Russian literature and some of the more obscure European publications. It would